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Taxonomic reassessment of *Hebius atemporalis* (Bourret, 1934) (Squamata, Natricidae), with the description of a new species from China

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Abstract

Hebius atemporalis (Bourret, 1934) has been reported from both northern Vietnam and southern China. Previous studies revealed deep genetic divergence between the Chinese and Vietnamese populations; however, no comprehensive taxonomic revision has examined the phylogenetic relationships and taxonomic status of these divergent lineages. Here, we present an integrative taxonomic reassessment of the *H. atemporalis* complex, combining detailed morphological comparisons and molecular data. As a result, we identify and describe a distinct new species, *Hebius malnatei* **sp. nov.**, endemic to the Yunnan-Guizhou Plateau, China. The new species can be distinguished from *H. atemporalis* sensu stricto by its larger adult body size, shorter relative tail length, higher numbers of ventrals and subcaudals, and distinctive coloration characterized by the absence of a nuchal collar. Phylogenetic analyses based on cytochrome *b* sequences consistently recover *Hebius malnatei* **sp. nov.** as the sister taxon of *H. atemporalis* s. str., with uncorrected *p*-distances of 8.0–9.8%. According to the IUCN Red List criteria, we recommend assigning *Hebius malnatei* **sp. nov.** to the category Least Concern (LC). This study highlights the need for taxonomic revision of widely distributed *Hebius* species and underscores the role of the Yunnan-Guizhou Plateau uplift in promoting species diversification.

Key Words

Cryptic diversity, cytochrome *b*, morphology, taxonomy, Yunnan-Guizhou Plateau

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Introduction

The keelback genus *Hebius* Thompson, 1913 (family Natricidae Bonaparte, 1840) represents the most diverse lineage of natricid snakes, comprising small- to medium-sized semi-aquatic or terrestrial taxa widely distributed across East and Southeast Asia (Guo et al. 2014; Ren et al. 2022; Xu et al. 2024; Bohra et al. 2025; Uetz et al. 2025). Members of *Hebius* are typically characterized by an elongate or moderately stout body, a weak but distinct head-neck demarcation, large eyes with round pupils, nasal in contact with 1st–2nd supralabials, posterior maxillary teeth moderately to markedly enlarged without diastema, and highly developed apical naked area on the hemipenis (Guo et al. 2014; Ren et al. 2018, 2022; David et al. 2023). Due to its high diversity, conserved morphology, and considerable intraspecific variation, species-level taxonomy remains challenging, frequently resulting in misidentifications and taxonomic ambiguities (David et al. 2015, 2021; Li et al. 2022; Bohra et al. 2025; Nguyen et al. 2025). Recent integrative analyses combining morphological and molecular data suggest that current species delimitations may substantially underestimate the true diversity within the genus, pointing to the presence of considerable cryptic lineages (e.g., Guo et al. 2014; Liu et al. 2018; Zhou et al. 2019; Hou et al. 2021; Li et al. 2022; Hauser et al. 2022; Ma et al. 2023; Xu et al. 2023, 2024; Gao et al. 2024; Nguyen et al. 2024, 2025). As currently recognized, the genus comprises 53 species, of which 30 are recorded from China and 11 from Vietnam (Bohra et al. 2025; Liu et al. 2025; Nguyen et al. 2025; Uetz et al. 2025). Among these species, the Tonkin Keelback, *Hebius atemporalis* (Bourret, 1934) is one of the few known to occur in both countries.

Hebius atemporalis (Bourret) was originally described as *Natrix atemporalis* by Bourret (1934) based on three specimens collected from Tonkin (now northern Vietnam), characterized by the absence of temporal scales. Malnate and Romer (1969) examined additional specimens from Hong Kong, China and confirmed the identification of the species with Bourret's (1934) material from Tam Dao National Park, Phu Tho Province, northern Vietnam, thereby extending its known distribution but without making any formal restriction of the type locality. Subsequently, the species has been variably assigned to *Amphiesma* Duméril, Bibron & Duméril (e.g. Zhao and Adler 1993; Zhao et al. 1998; Zhao 2006; Yang and Rao 2008; Nguyen et al. 2009) until Guo et al. (2014), based on molecular phylogenetic and morphological evidence, transferred it to *Hebius* Thompson, a treatment now widely followed (e.g., Poyarkov et al. 2023; Nguyen et al. 2024, 2025; Uetz et al. 2025). *Hebius atemporalis* has been widely reported across northern Vietnam and southern China (e.g., Zhao et al. 1998; Zhao, 2006; Nguyen et al. 2009; Wallach et al. 2014; Nguyen and Poyarkov 2020; Li et al. 2023). Diagnostic features of specimens traditionally assigned to *Hebius atemporalis* species complex include 17-17-17 dorsal scale rows weakly keeled except for the outermost 1–6 rows, absence of temporal scales, a white ventral head surface with scattered black spots or streaks, strongly black-edged infralabial sutures, a distinct white or orange nuchal collar, and a dorsal coloration grading from reddish to dark brown anteriorly to blackish brown posteriorly (Bourret 1934; Malnate and Romer 1969; Zhao et al. 1998; Li et al. 2023).

Despite its seemingly wide distribution, *Hebius atemporalis* remains poorly studied, and few works have addressed the taxonomic status or phylogenetic placement of its geographically disparate populations. In Vietnam, confirmed records are limited to Phu Tho, Tuyen Quang, Dien Bien, and Nghe An provinces, whereas in China it has been documented from Guangdong, Guizhou, Yunnan provinces, and Guangxi Zhuang Autonomous Region as well as Chongqing Municipality (Zhao et al. 1998; Zhao 2006; Nguyen et al. 2009; Nguyen and Poyarkov 2020; Li et al. 2023; this study). Previous molecular phylogenetic studies (e.g., Li et al. 2022; Deepak et al. 2022) revealed two deeply divergent clades within *H. atemporalis*, suggesting a need for taxonomic reevaluation. Within this complex framework, the *H. atemporalis* species complex has long posed particular challenges, as subtle morphological differentiation and limited sampling have hindered robust species delimitation. In this study, we use both newly sampled specimens across Vietnam and China and museum collections to conduct a comprehensive taxonomic revision of this widely distributed yet understudied taxon. Integrating detailed morphological assessments and molecular phylogenetic analyses, we identify a distinct and previously unrecognized lineage endemic to the Yunnan-Guizhou Plateau. Herein, we describe this lineage as a new species and discuss the potential influence of regional uplift events on its diversification.

Materials and methods

Morphological comparison

A total of 27 preserved specimens of *Hebius atemporalis* sensu lato (including two syntypes MNHN-RA-1935.77–78, Fig. 1), including 12 newly sampled specimens collected from Vietnam and China during our field work from 2020 to 2025 were examined for external morphological characters (Table 1).

Methodology of definitions and measurements of morphological characters were based on Zhao (2006) and Ren et al. (2022). The total length (TL), snout-vent length (SVL), and tail length (TaL) were measured using a measuring tape to the nearest 1.0 mm. The head length (HL) and head width (HW) were taken with a slide-caliper to the nearest 0.1 mm. We inspected pholidosis counts including number and arrangement of internasal (IN), prefrontal (PrF), loreal (L), frontal (F), parietal (P), preocular (PrO), postocular (PtO), supralabial (SL), infralabial (IL), temporal (TEM), dorsal scale rows (DSR), ventral (VEN), subcaudal (SC). The number and shape of maxillary teeth (MT), and keeling status of the dorsal scale rows (KDSR) were examined under a dissecting microscope.

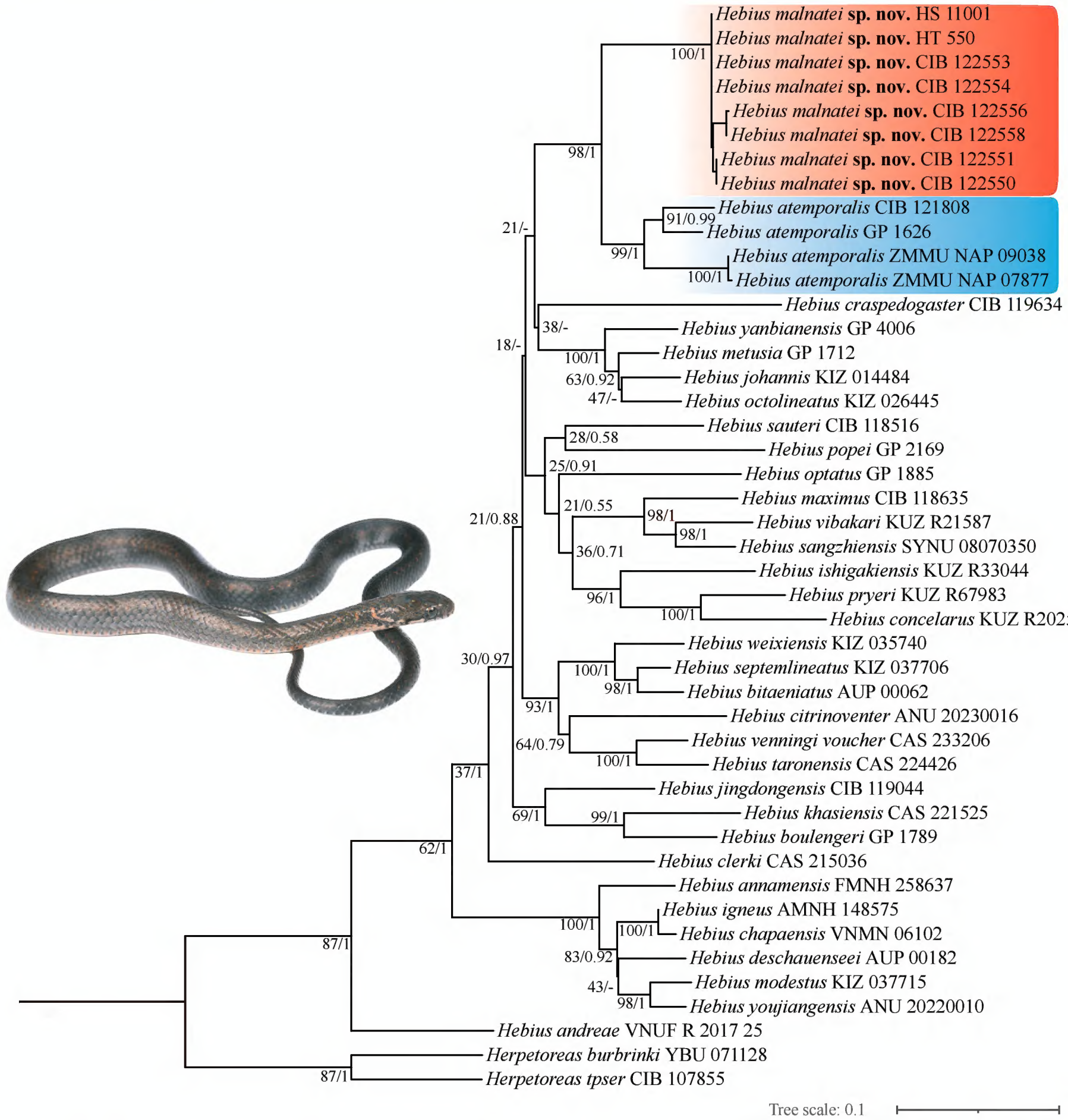

Figure 1. Maximum-likelihood (ML) phylogenetic tree of *Hebius* species based on Cyt *b* gene fragments. Bayesian posterior probabilities (BPP) and bootstrap approximation (BSP) were denoted beside each node (BSP/BPP, "-" indicates conflicting topologies between BI and ML phylogenetic trees).

Molecular analyses

Genomic DNA was extracted from muscle or liver tissue with Ezup Column Animal Genomic DNA Purification Kit (Sangon Biotech, China) using a standard method provided by the manufacturer. We amplified mitochondrial cytochrome *b* gene (Cyt *b*) sequences using primers L14919 (5-AACCACCGTTGTACATCAACT-3) and H16064 (5-CTTTGGCTTACAAGAACAATGCTTTA-3) (Burbrink et al. 2000). PCR amplification scheme followed Li et al. (2022). The PCR products were purified and then sequenced in both directions by Sangon Biotech Co., Ltd. (Shanghai, China). Sequences' alignment and calculation of the uncorrected pairwise distance (*p*-distance) were conducted by using MEGA X (Kumar et al. 2018). PartitionFinder2 was used to search for the best nucleotide substitution model based on Bayesian Information Criterion (BIC) and employed a greedy search strategy (Lanfear et al. 2017). All newly sequenced Cyt *b* sequences were uploaded to GenBank (Suppl. material 1: table S1). An additional 36 congeneric *Hebius* sequences and two outgroup taxa (*Herpetoreas burbrinki* Guo, Zhu, Liu, Zhang, Li, Huang & Pyron and *Herpetoreas tpser* Ren, Jiang, Huang, David & Li) sequences were obtained from GenBank (Suppl. material 1: table S1).

Phylogenetic analysis was conducted using Maximum Likelihood (ML) and Bayesian Inference (BI) method. BI analysis was conducted by using MrBayes v3.2.6 (Ronquist et al. 2012) under the best nucleotide substitution model (GTR+I+G), run for 2,000,000 generations with

Table 1. Main measurements and meristic characters of *Hebius malnatei* sp. nov. and *H. atemporalis* examined in this study. Abbreviations: F = adult female; M = adult male; SF = subadult female; SM = subadult male; J = juvenile; n/a = not available.

Voucher number	Sex	Locality	Status	SVL (mm)	TaL (mm)	MT	PrO	PtO	L	SL	SL-E	SL-P	IL	AT	DSR	VEN	SC
***Hebius malnatei* sp. nov.**																	
YBU 14259	SF	Mingjiu, Mengzi, Yunnan, China		286	86	26	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	1/1	17-17-17	152	60
CIB 72560	SM	Yunnan, China		282	93	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/7	1/1	17-17-17	147	70
CIB 101974	M	Mengzi, Honghe, Yunnan, China	Paratype	362	101	29	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	1/1	17-17-17	154	66
CIB 122550	F	Pugu, Panzhou, Liupanshui, Guizhou, China	Paratype	416	125+	27	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	0/0	17-17-17	150	61+
CIB 122551	F	Pugu, Panzhou, Liupanshui, Guizhou, China	Holotype	379	112	26	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	1/0	17-17-17	151	63
CIB 122552	F	Mengzi, Honghe, Yunnan, China	Paratype	346	104	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	0/0	17-17-17	150	63
CIB 122553	F	Mengzi, Honghe, Yunnan, China	Paratype	327	120	26	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/6	1/1	17-17-17	153	66
CIB 122554	F	Honghe, Yunnan, China	Paratype	326	103	n/a	1/2	2/2	1/1	6/6	3–4/3–4	5/5	7/7	0/1	17-17-17	153	66
CIB 122555	SF	Mengzi, Honghe, Yunnan, China		286	96	26	1/1	2/2	1/1	5/5	3/3	4/4	6/6	0/1	17-17-17	155	68
CIB 122556	J	Panlong, Kunming, Yunnan, China		139	47	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	1/1	17-17-17	146	66
CIB 122557	M	Mengzi, Honghe, Yunnan, China	Paratype	305	99+	28	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	0/0	17-17-17	156	67+
CIB 122558	SF	Panlong, Kunming, Yunnan, China	Paratype	200	63	28	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	1/1	17-17-17	147	64
Hebius atemporalis																	
MNHN-RA-193578	F	Tam Dao NP, Phu Tho, Vietnam	Syntype	265	n/a	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	0/0	17-17-17	136	63
MNHN-RA-193577	M	Tam Dao NP, Phu Tho, Vietnam	Syntype	266	118	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	1/1	17-17-17	131	72
ZMMU NAP-09038	M	Pu Hoat NR, Nghe An, Vietnam		247	107	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	1/1	17-17-17	127	74
ZMMU NAP-07877	M	Pu Hoat NR, Nghe An, Vietnam		266	50+	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	1/1	17-17-17	124	n/a
MNHN-RA-1958.0462	M	Tam Dao NP, Phu Tho, Vietnam		242	117	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	1/1	17-17-17	130	79
MNHN-RA-1958.0461	M	Tam Dao NP, Phu Tho, Vietnam		211	91	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	1/1	17-17-17	127	71
MNHN-RA-1938.0120	M	Tam Dao NP, Phu Tho, Vietnam		220	96	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	0/0	17-17-17	126	72
MNHN-RA-1938.0119	M	Tam Dao NP, Phu Tho, Vietnam		265	n/a	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	0/0	17-17-17	123	n/a
MNHN-RA-1935.0450	M	Tam Dao NP, Phu Tho, Vietnam		260	n/a	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	1/1	17-17-17	129	n/a
DTU 424	F	Pu Mat NP, Nghe An, Vietnam		292	135	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	1/1	17-17–17	136	70
ZFMK 87277	M	Tam Dao NP, Phu Tho, Vietnam		291	132	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	1/1	17-17-17	134	75
CIB 8447	F	Mangshan, Yizhang, Chenzhou, Hunan, China		194	84	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	6/6	1/1	17-17-17	132	74
CIB 8449	F	Youyang, Chongqing, China		294	37+	32	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/6	1/1	17-17-17	140	20+
CIB 121808	J	Yaogu, Libo, Qiannan, Guizhou, China		93	38+	n/a	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	1/1	17-17-17	134	69
CIB 121809	F	Wufeng, Yichang, Hubei, China		215	86	33	1/1	2/2	1/1	6/6	3–4/3–4	5/5	7/7	1/1	17-17-17	134	72

4 chains across 2 runs, sampling every 100 generations, the first 25% trees were discarded as "burn in". Average standard deviation of split frequencies was checked to reach < 0.01 when the running process is finished. ML analysis was performed using IQ-TREE (Nguyen et al. 2015), set with the same nucleotide substitution model as in BI analysis with 1,000 bootstraps.

Other abbreviations: AR = Autonomous Region; NP = National Park; NR = Nature Reserve; NNR = National Nature Reserve; Mt = Mountain (s); SAR = Special Administrative Region; a.s.l. = above sea level. Suppl. material 1: table S2 lists the museum and natural history collection acronyms used or mentioned in this study.

Results

Molecular phylogeny

The aligned Cyt *b* dataset comprised 1,098 base pairs. Both Bayesian Inference (BI) and Maximum Likelihood (ML) analyses yielded largely congruent topologies across most lineages, although relationships among deeper branches remained unresolved. *Hebius atemporalis* sensu lato was recovered as a strongly supported monophyletic group (ML bootstrap support [BS] = 98; Bayesian posterior probability [BPP] = 1.0), forming a inferiorly supported sister relationship with the clade comprises *H. craspedogaster*, *H. yanbianensis*, *H. metusia*, *H. johannis*, and *H. octolineatus.* (BS = 21) (Fig. 1). Within this clade, the putative new species from the Yunnan-Guizhou Plateau, southwestern China was recovered as a highly divergent lineage, separated from *H. atemporalis* sensu stricto (found elsewhere in China and northern Vietnam) by an uncorrected *p*-distance of 8.0–9.8% based on Cyt *b* sequences. In contrast, genetic divergence within the Yunnan-Guizhou population was low, with *p*-distances less than 1% (Suppl. material 1: table S3). Notable divergence is also observed in *H. atemporalis* sensu stricto, with *p*-distances of 6.4–7.0% between Chinese and Vietnamese populations, and 4.4% between Guizhou and Guangdong populations in China.

Morphology

Morphological assessment identified a consistent suite of characters that clearly distinguishes the Yunnan-Guizhou Plateau population from *H. atemporalis* sensu stricto and all other congeners. Including temporal scale arrangement, dorsal scale rows, ventral scale counts, and color-

ation described below. Molecular phylogenetic analyses corroborate its independent status by consistently placing it as the sister taxon of *H. atemporalis* sensu stricto. Here, we identify this lineage as a new species endemic to the Yunnan-Guizhou Plateau. Additionally, owing to the lack of a detailed morphological description for true *Hebius atemporalis*, we provide a redescription of this species based on syntypes and additional materials, alongside the description of the new species.

Taxonomic account

Hebius atemporalis (Bourret, 1934)

Tables 1, 2, Figs 2–5

Syntypes. MNHN-RA-1935.0077–0078. Type locality: "Tonkin" [i.e., now northern Vietnam]. Bourret (1934) gave the type locality as Tonkin; later authors (e.g., Malnate and Romer 1969) referred to Tam Dao National Park, Phu Tho Province, northern Vietnam, but this does not constitute a formal restriction under the ICZN.

Examined material (n = 15). The two syntypes and 13 additional specimens of *Hebius atemporalis* were examined in this study (see Table 1).

Revised diagnosis. *Hebius atemporalis* can be distinguished from its congeners by the following combination of characters: (1) small body size, maximum snout-vent length 294 mm; (2) head small, narrow, and moderately distinct from neck; (3) maxillary teeth 27–36, gradually enlarged posteriorly; (4) supralabials 6, with the 3rd and 4th entering the orbit; (5) temporal scale absent or represented by a small narrow scale; (6) infralabials 6–7; (7) dorsal scale rows 17-17-17, weakly keeled except for the outermost 1–6 rows; (8) ventrals 123–140; (9) subcaudals 63–79, paired; (10) ventral surface of head white, scattered with black spots or streaks; (11) sutures of infralabials strongly edged in black; (12) a white to orangish nuchal collar present; (13) dorsal ground color gradually changing from reddish brown or dark brown anteriorly to blackish brown posteriorly (based on data of Bourret (1934); Malnate and Romer (1969); this study).

Table 2. Comparison of morphological characters of *Hebius malnatei* sp. nov. with *H. atemporalis*, based on data from the present study. Diagnostic differences from the new species are indicated in bold.

Species	*Hebius malnatei* sp. nov.	*Hebius atemporalis*
max SVL	**416 mm (n = 12)**	**294 mm (n = 15)**
Ratio TaL/TL	**0.22–0.27 (0.24 ± 0.01, n = 10)**	**0.28–0.33 (0.30 ± 0.01, n = 11)**
VEN	**146–156 (151.17 ± 3.27, n = 12)**	**123–140 (130.87 ± 4.88, n = 15)**
SC	60–70 (65.20 ± 2.82, n = 10)	63–79 (71.91 ± 4.01, n = 11)
VEN+SC	**211–223 (216.00 ± 4.14, n = 10)**	**198–209 (203.45 ± 4.08, n = 11)**
MT	26–29	27–36
AN	divided	divided
DSR	17-17-17	17-17-17
SL	6 (rarely 5)	6
SL-E	3–4 (rarely 3)	3–4
IL	7 (rarely 6)	7 or 6
PrO	1	1
PtO	2	2
TEM	0+1 or 0+2	1+1 or 0+1
Anterior body coloration	**brown**	**brownish red**
Neck collar	**absent**	**white to orange collar present**

Description (based on 15 examined materials). Head small, narrow, and moderately distinct from neck (HL/HW 1.65–2.18); body slender, with maximum total length 427 mm; tail length 28–33% of total length. Eye moderate, with round pupil.

Body scalation. Dorsal scales in 17-17-17 rows; anterior rows smooth or weakly keeled on the upper 5–11 rows, midbody and posterior rows weakly keeled except the outermost 1–3 rows; ventrals 123–140 (123–134 in males, 132–140 in females); cloacal plate divided; subcaudals 63–79 (63–74 in females, 71–79 in males), paired.

Head scalation. Rostral broad, visible from above, slightly projecting between internasals; internasals paired, nearly triangular, broader than long, broadly in contact medially, curved outward, not contacting loreal; prefrontals paired, pentagonal, rather large, wider than long, bordering loreal laterally and preocular and supraocular posteriorly; frontal hexagonal, distinctly longer than wide, posteriorly embedded into parietals; parietals paired, much longer than wide; nasals wider than high, divided below nostril, contacting 1st–2nd supralabials; loreal single, quadrangular, about as wide as high, bordering 2nd–3rd supralabials (2nd only in ZMMU NAP-07877 and right side of CIB 8447), not entering orbit; preocular single, much higher than wide; supraocular single, elongated, narrowing anteriorly, in contact with parietal posteriorly; postoculars 2, the upper markedly larger and broader than the lower; temporal scale absent or represented by a small narrow scale enclosed by postoculars, parietal, and 5th supralabial; supralabials 6, first four gradually increasing in size posteriorly, 3rd–4th entering orbit, 5th largest, dorsal border contacting parietal; infralabials 6–7, first pair in broad contact behind mental, 1st–4th contacting anterior chin shields; chin shields pairs two, anterior pair in broad contact medially; posterior pair longer and contacting anterior pair.

Coloration and pattern. In life, dorsal head dark brown; internasals and prefrontals light brown, scattered with small black dots (CIB 121809 bears a worm-like yellow pattern on head), a pair of irregular light spots present symmetrically along parietal suture; supralabials 1st–4th white with strong black edging, 5th brownish with a large black-edged white elliptical spot anteriorly, 6th dark brown occasionally with a small white dorsal spot; a white or orange collar present on the neck, separated from parietal suture by 3–4 dorsal scales, usually 1–3 scales wide, wider dorsally, sometimes broken medially, and occasionally extending slightly posteriorly; dorsal surface of body and tail color reddish to dark brown anteriorly, gradually darkening to blackish brown or dark olive posteriorly, speckled with small dark blotches and spots; a

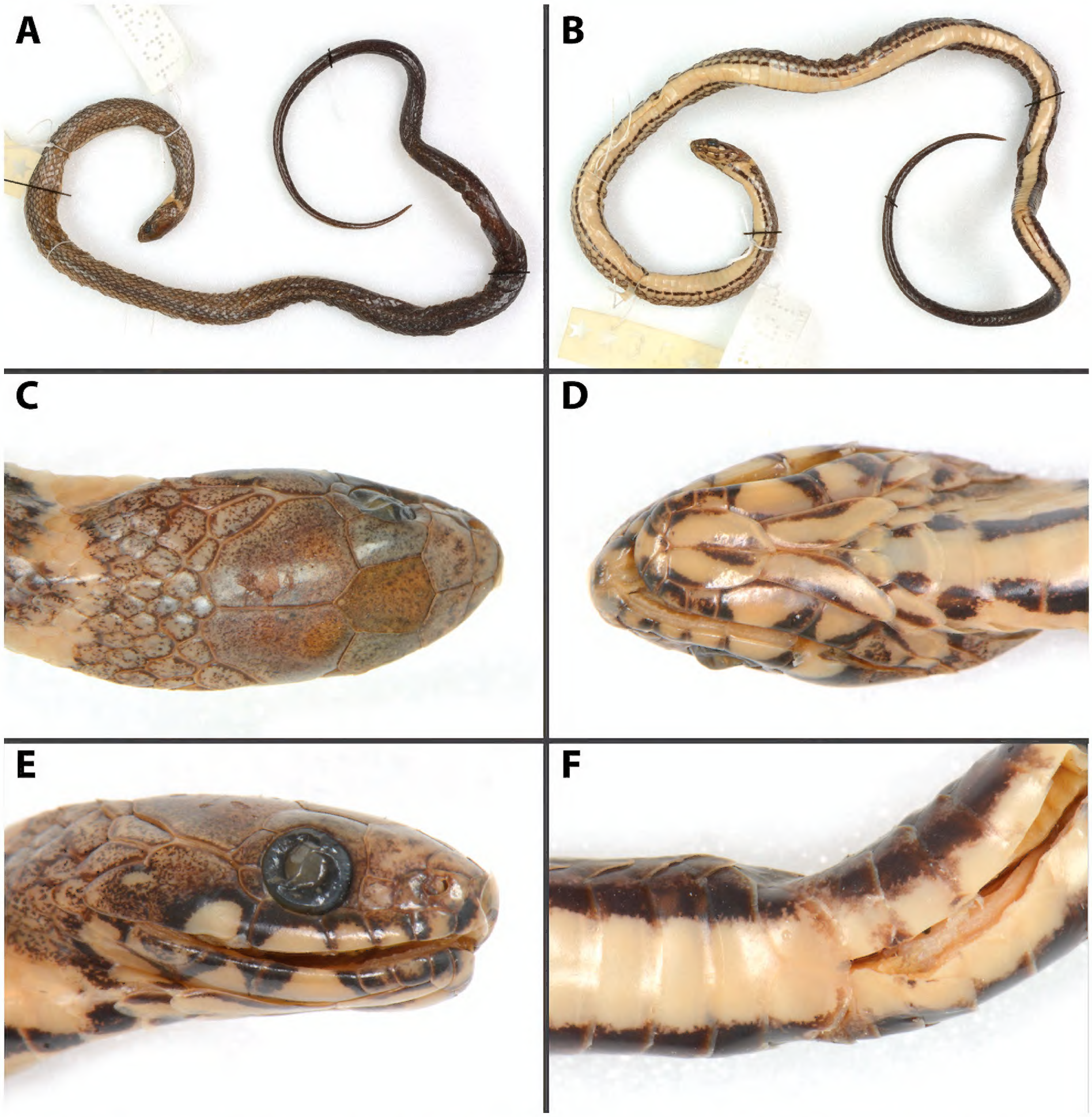

Figure 2. *Hebius atemporalis* in preservative, specimen MNHN-RA-1935.77 (syntype, adult male): general dorsal view (**A**); general ventral view (**B**); dorsal view of the head (**C**); ventral view of the head (**D**); lateral view of the head, right side (**E**); ventral view of the cloacal region (**F**). Photograph by J. Courtois.

series of light spots on the 3rd–5th dorsal scale rows, separated by 1–2 scales, extends posteriorly from behind the collar, fading or becoming indistinct towards the tail; ventral surface of head white, scattered with black spots or streaks; infralabial sutures strongly black-edged; ventral surface of body and tail white to pale yellow, with two series of black dots of variable intensity along the lateral margins of ventrals and subcaudals. In preservative, overall pattern similar as in life, though dorsal brown tones darken slightly, the neck collar and yellowish lateral spots fade to pale white, and ventral surfaces become uniformly pale white.

Dentition. Maxillary teeth 27–36, without diastema, gradually enlarged posteriorly (data from Malnate and Romer 1969; this study).

Distribution. *Hebius atemporalis* sensu stricto is confirmed from northern Vietnam (including Phu Tho, Tuyen Quang, Dien Bien, and Nghe An) and southern and central China (including Hong Kong, Guangdong, Guangxi, Guizhou, Hunan, Hubei and Chongqing), occurring at elevations of 400–1,700 m a.s.l. (Fig. 5). Several additional records from other regions remain unverified. For instance, Deuve (1970) reported the species from Laos, but without providing voucher specimens or supporting data.

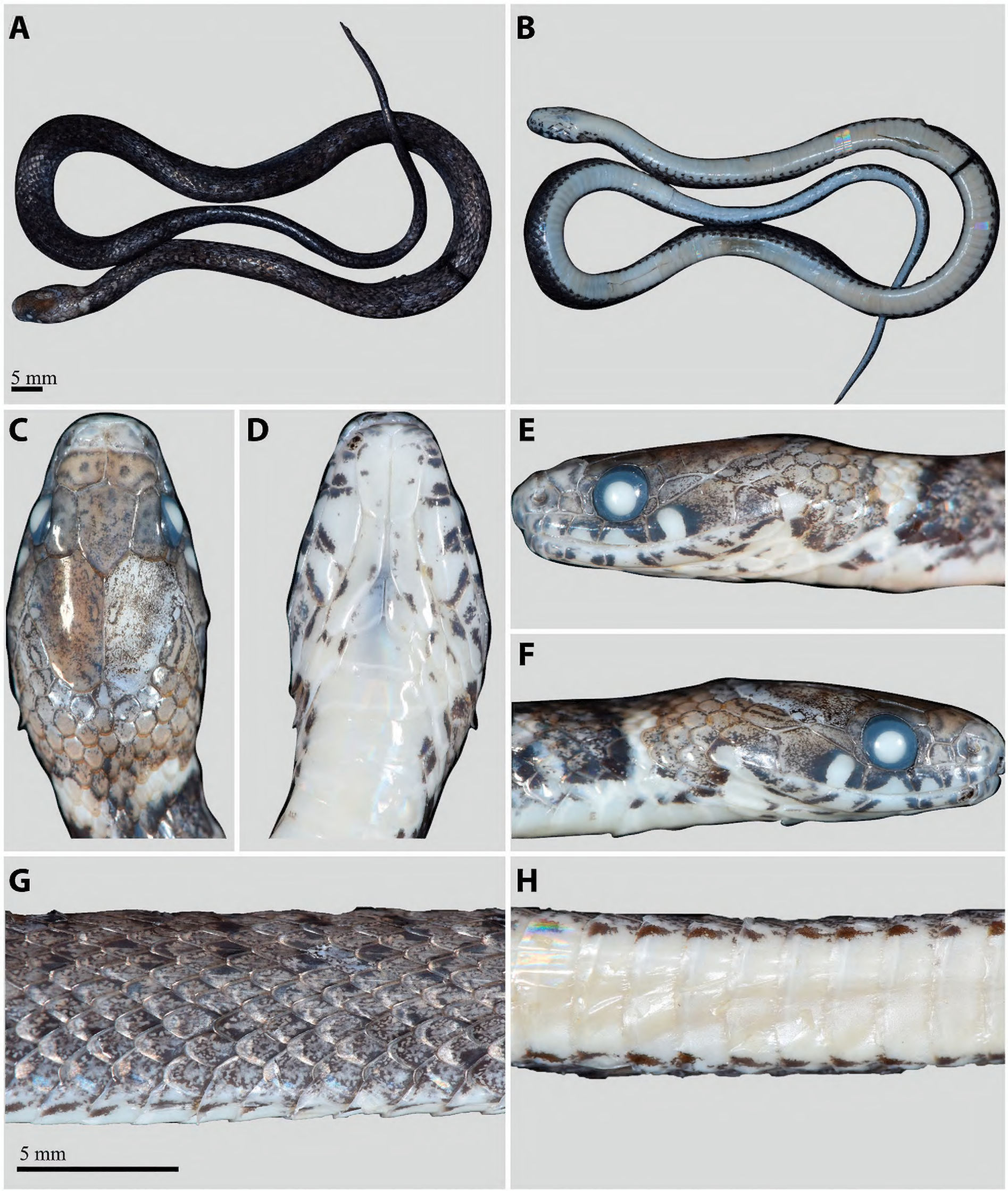

Figure 3. *Hebius atemporalis* in preservative, specimen CIB 121809 (adult female): general dorsal view (**A**); general ventral view (**B**); dorsal view of the head (**C**); ventral view of the head (**D**); lateral view of the head, right side (**E**); lateral view of the head, left side (**F**); midbody dorsal scales (**G**); midbody ventral scales (**H**). Photographs by J.J. Huang.

David et al. (2023) subsequently clarified that the presence of *H. atemporalis* in Laos remains unconfirmed. In contrast, populations from the Yunnan-Guizhou Plateau (Guizhou and Yunnan, China), previously referred to *H. atemporalis*, are morphologically and genetically distinct, and are herein recognized as a new species, formally described below.

Natural history notes. *Hebius atemporalis* inhabits low- to mid-elevation subtropical montane regions and appears to tolerate a variety of habitats. In Vietnam, a specimen from Pu Mat NP, Nghe An Province (950 m a.s.l.), was found on the ground at ca. 16 h 30 in secondary evergreen forest with dense shrubs. In China, one

Figure 4. Photographs in life of *Hebius atemporalis*. In Vietnam: ZMMU NAP-09038 from Pu Hoat NR, Nghe An (**A**); Muong Nhe NR, Dien Bien (**B**); Pu Mat NP, Nghe An (**C**); Mt. Tay Con Linh, Tuyen Quang (**F**). In China: CIB 121809 from Houhe, Wufeng, Yichang, Hubei (**E**); Tsuen Wan, Hong Kong (**D**). Photographs by N.A. Poyarkov (**A**), reproduced from Le et al. (2014) (**B**), T.V. Nguyen (**C**), C.D. Trieu (**D**), C.L. Li (**E**), A. Tomaszek (**F**).

specimen from Houhe NNR, Hubei Province was collected near a forested stream, whereas Malnate and Romer (1969) reported individuals from Hong Kong SAR near the summit of Tai Mo Shan (ca. 914 m a.s.l.) in a comparatively dry environment without streams. The species therefore appears to occupy both primary and secondary montane forest habitats. Activity is mainly diurnal, with most specimens collected during the day, although some remain active into the late afternoon. When disturbed, individuals move rapidly and emit a strong, unpleasant odor as a defensive behavior. Its diet remains poorly known, but it is presumed to feed primarily on earthworms.

Hebius malnatei Li, Nguyen, Huang, Poyarkov, David, Li & Ren, sp. nov.

https://zoobank.org/F80B5CA2-AF77-4BBD-BE1A-EA627ED48745

Chresonymy. *Natrix atemporalis* — Wu (1985: 171, in part)

Amphiesma atemporale — Wallach et al. (2014: 28, in part)

Amphiesma atemporalis — Zhao and Adler (1993: 225, in part); Zhao et al. (1998: 52, in part); Zhao (2006: 45 in part); Yang and Rao (2008: 252, in part)

Hebius atemporale — Guo (2014, in part)

Hebius atemporalis — David et al. (2021: 54, in part)

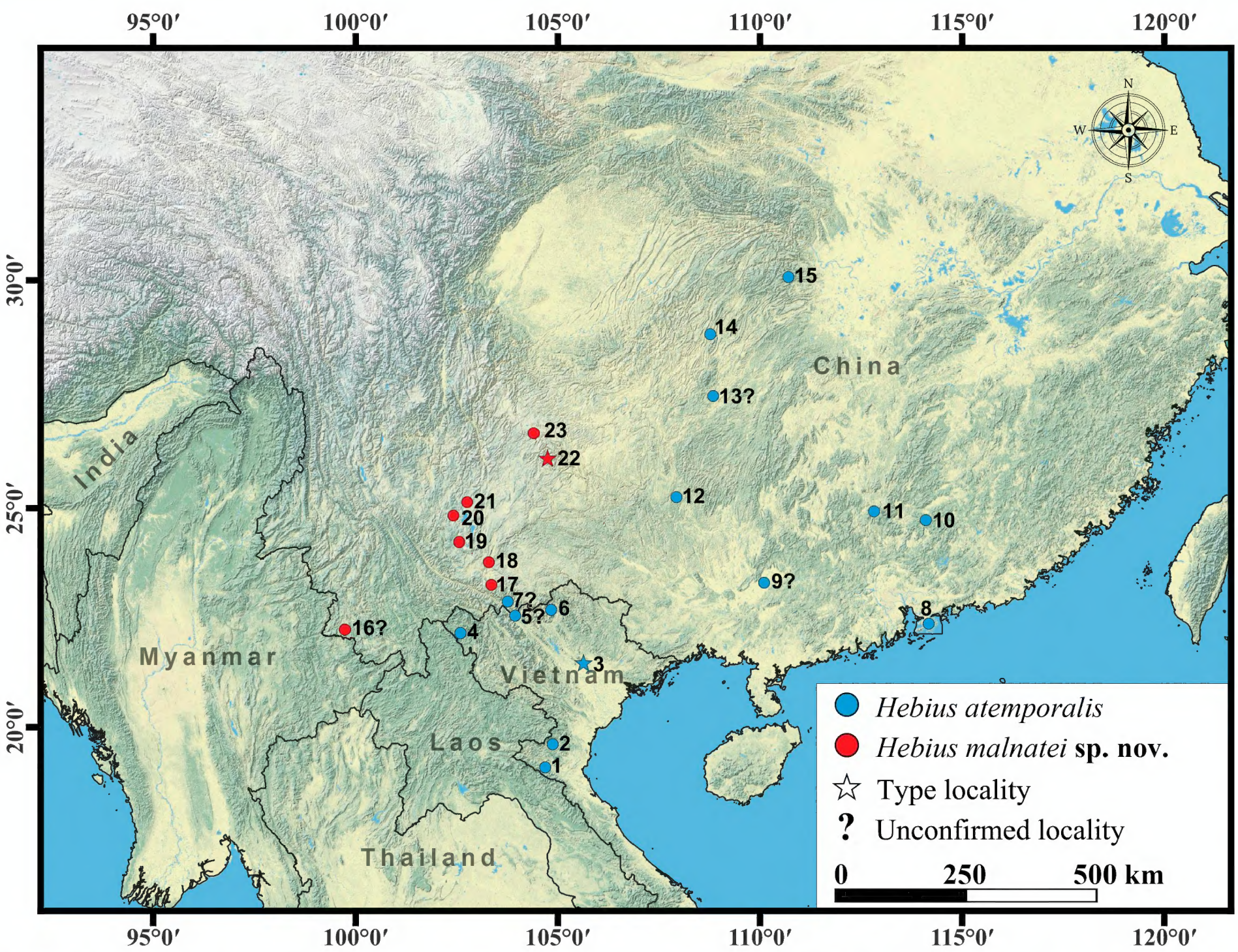

Figure 5. Distribution map of the *Hebius atemporalis* complex. *H. atemporalis*: 1 – Pu Mat NP, Nghe An, Vietnam; 2 – Pu Hoat NR, Nghe An, Vietnam; 3 – Tam Dao NP, Phu Tho, Vietnam (type locality); 4 – Muong Nhe NR, Dien Bien, Vietnam; 5 – Hekou, Honghe, Yunnan, China; 6 – Mt. Tay Con Linh, Tuyen Quang, Vietnam; 7 – Pingbian, Honghe, Yunnan, China; 8 – Hong Kong, China; 9 – Guiping, Guangxi, China; 10 – Chebaling, Shixing, Shaoguan, Guangdong, China; 11 – Mangshan, Yizhang, Chenzhou, Hunan, China; 12 – Yaogu, Libo, Guizhou, China; 13 – Jiangkou, Tongren, Guizhou, China; 14 – Youyang, Chongqing, China; 15 – Houhe, Wufeng, Yichang, Hubei, China. *Hebius malnatei* sp. nov.: 16 – Menglian, Puer, Yunnan, China; 17 – Mengzi, Honghe, Yunnan, China; 18 – Kaiyuan, Honghe, Yunnan, China; 19 – Yuxi, Yunnan, China; 20–21 – Kunming, Yunnan, China; 22 – Pugu, Panzhou, Liupanshui, Guizhou, China (type locality); 23 – Weining, Bijie, Guizhou, China.

Holotype. CIB 122551, adult female, from Pugu Village, Panzhou County, Liupanshui City, Guizhou Province, China (26.0564°N, 104.7504°E; elevation 1,750 m a.s.l.), collected on 12 May 2024, collected by locals.

Paratypes. (n = 5, all from China). CIB 122558 (subadult female) from Panlong District, Kunming City, Yunnan Province (25.1430°N, 102.7486°E); CIB 122557 (adult male), CIB 101974 (adult male), CIB 122552 (adult female) from Mengzi City, Honghe Prefecture, Yunnan Province; and CIB 122550 (adult female) from Pugu Village, Panzhou County, Liupanshui City, Guizhou Province.

Additional specimens. (n = 6, all from Yunnan Province, China). CIB 122553 (adult female), CIB 122554 (adult female), CIB 122555 (subadult female) from Mengzi City, Honghe Prefecture; YBU 14259 (subadult female) from Mingjiu Town, Mengzi City, Honghe Prefecture; CIB 122556 (juvenile, sex unknown) from Panlong District, Kunming City; and CIB 72560 (subadult male) from Yunnan Province (exact locality unknown).

Diagnosis. *Hebius malnatei* sp. nov. is distinguished from all congeners by the following combination of characters: (1) small body size, maximum snout-vent length 416 mm; (2) head small, narrow, and moderately distinct from neck; (3) maxillary teeth 26–29, gradually enlarged posteriorly; (4) supralabials 6 (rarely 5), with the 3rd and 4th entering the orbit; (5) temporal scale absent or represented by a small narrow scale; (6) infralabials 7 (rarely 6); (7) dorsal scale rows 17-17-17, weakly keeled except for the outermost 1–6 rows; (8) ventrals 146–156 with two preventrals; (9) subcaudals 60–70, paired; (10) ventral surface of head white, scattered with black spots or streaks; (11) sutures of infralabials strongly edged in black; (12) a white to orangish nuchal collar absent; (13) dorsal ground color gradually

changing from brown to dark olive, usually with a series of discontinuous light spots along the lateral side, forming an inconspicuous stripe; (14) tail relatively short (TaL/SVL ratio 0.22–0.27).

Description of the holotype. (Table 1, Figs 6, 7). Head narrow and elongate, subrectangular, distinctly separated from neck, with a slight flattening anterior to the eyes, HL/HW 1.78; snout short, slightly longer than the horizontal diameter of the eye, slightly flattened and narrowing anteriorly, tip nearly blunt in dorsal view and rounded in lateral view with a well-defined canthus rostralis; eyes relatively large, diameter clearly exceeding vertical distance from its lower margin to edge of upper lip, pupil round; body relatively slender and subcylindrical; tail cylindrical, long, and thin, tapering progressively toward the tip.

Dentition. Maxillary teeth 26, without diastema, gradually enlarged posteriorly.

Body size. SVL 379 mm; TaL 112 mm; TL 491 mm; ratio TaL/TL = 0.23.

Body scalation. Dorsal scales in 17-17-17 rows, most scales smooth, with feeble keels present except outer six rows at anterior body and outer four rows at mid and posterior body, becoming more distinct along the mid-dorsum, scales of the 1st dorsal row enlarged; apical pits absent; ventrals 151, preceded by 2 preventrals; cloacal plate divided; subcaudals 63, all paired.

Head scalation. Rostral rectangular, wider than high, slightly visible from above (anterior margin partly damaged); nasal large, rectangular, distinctly longer than high, divided into anterior and posterior sections, bordered by first two supralabials, rostral, internasal, and prefrontal, nostril round, piercing anterior edge of posterior section of nasal; internasals two, subrectangular, slightly curved, slightly wider than long, in contact with rostral anteriorly, nasals laterally, and prefrontals posteriorly; prefrontals two, large, subrectangular, shorter than frontal, clearly visible in lateral view, each in contact with internasal, nasal, preocular, loreal, and frontal; frontal hexagonal, elongate, tapering posteriorly, about 1.5 times as long as wide, equal in length to distance from tip of snout to its anterior margin; parietals elongate, longer than wide, in broad medial contact, length slightly exceeding that of frontal; supraoculars 1/1, distinctly longer than wide, in contact with prefrontals; loreals 1/1, small, rectangular, not entering orbit, bordered by the second supralabial; preoculars 1/1, large, more than twice as high as wide, broadly in contact with the prefrontal; subocular absent; postoculars 2/2, arranged vertically, decreasing in size from dorsal to ventral; temporals 1+1/0+1, anterior temporal on right side narrow, not entering orbit, sharply pointed posteriorly, bordered by 5th supralabial and parietal, posterior temporal fan-shaped, bordered dorsally by parietal and ventrally by 5th and 6th supralabials on right side and separated from 6th supralabial by a small fan-shaped scale situated between temporal and 6th supralabial on left side; supralabials 6/6, first and second in contact with nasal, second also contacting loreal, third to fourth entering orbit, fifth largest, in contact with parietal; infralabials 7/7, first pair in broad medial contact, first to fourth in contact with anterior chin shields; posterior chin shields longer than anterior chin shields, separated medially by two small scales.

Coloration. In life, dorsal surface of head dark brown with irregular lighter mottling on rostral and internasals; snout light brown; supralabials cream white, first to fourth with grey to black pigmentation on the upper and lateral surfaces, fifth with the right half concolorous with the dorsal head, sixth bordered by a distinct dark-grey margin; dorsal coloration of body and tail gradually changes from brown on the anterior body to dark olive at posterior body and tail, slightly lighter laterally, a series of light orangish spots, continuous or separated by one or two dorsal scales, present on four to six body scale rows from neck to tail tip, gradually smaller and vaguer posteriorly, forming an indistinct lateral stripe, faint and irregular darker spots indistinctly visible along body and tail; ventral surface of head cream white, with irregular black spots and streaks along the edges of chin shields and adjacent small scales; infralabials cream white, sutures conspicuously black-edged, the first to third densely scattered with grey to black dots, fourth to seventh black on the upper edge and sparsely dotted with black; ventral surface of neck and anterior body faint yellow gradually transitioning to white on posterior body and tail, the lateral margins of the ventral scales concolorous with the dorsal scales, a series of indistinct small black spots present along each side of the ventrals, forming a chain-like pattern; subcaudals cream white with dark brown mottling, forming irregular lateral patches toward the tail tip. In preservative, coloration resembles the living status, except the dorsal coloration become darker and ventral of head, body, and tail are uniformly pale white.

Variation (Fig. 7). Measurements and scalation data for the type series and additional specimens are summarized in Table 1. Snout-vent length 139–416 mm; tail length 47–125+ mm (0.22–0.27 of total length). Maxillary teeth 26–29. Dorsal scale rows weakly keeled on 7–15 upper rows at midbody. Postoculars 2–3; anterior temporal variable, 1/0, 0/1 or 0/0; supralabials usually 6 (rarely 5), with the 3rd and 4th entering the orbit; infralabials 6–7 (rarely 5/5 in CIB 122555), with the first four contacting the anterior chin shields; ventrals 146–156; subcaudals 60–70, all paired.

Coloration generally matches the holotype with the following variations: (1) some individuals (e.g. CIB 122554) exhibit a more brownish dorsal head compared to the dorsal body; (2) the degree of ventral head spotting varies slightly, with some specimens (e.g., CIB 122550) exhibiting denser pigmentation whereas others (e.g., CIB 72560) display only faint, obscure markings; (3) the ventral surfaces of the body and tail sometimes bear scattered black margins on ventral and subcaudal scales, with black spots along the lateral edges of ventral scales being more distinct in certain specimens (e.g., CIB 122555).

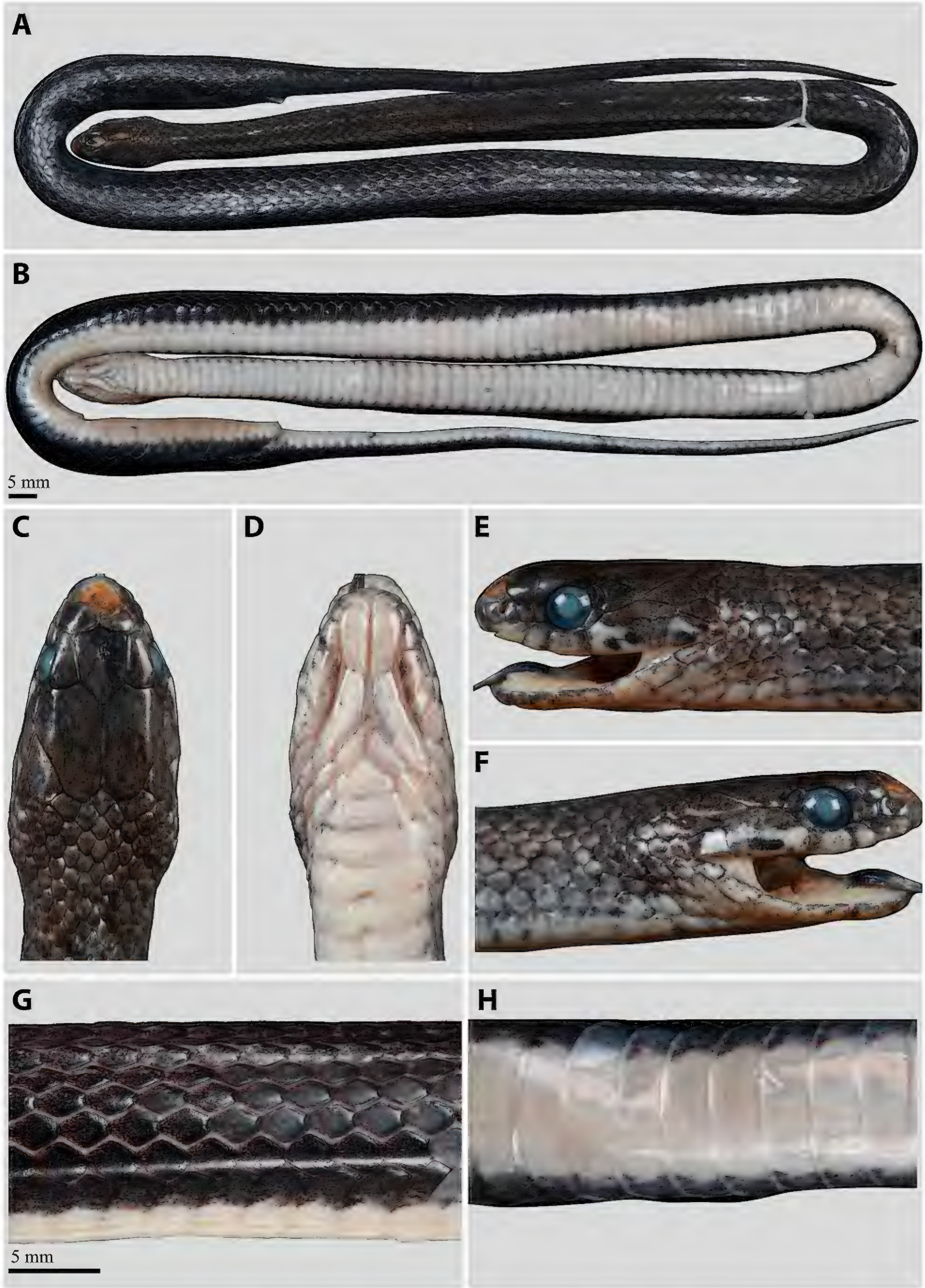

Figure 6. *Hebius malnatei* sp. nov. in preservative, specimen CIB 122551 (holotype, adult female): general dorsal view (**A**); general ventral view (**B**); dorsal view of the head (**C**); ventral view of the head (**D**); lateral view of the head, right side (**E**); lateral view of the head, left side (**F**); midbody dorsal scales (**G**); midbody ventral scales (H). Photographs by J.J. Huang.

Figure 7. Photographs in life of *Hebius malnatei* sp. nov. from China: CIB 122551, Pugu, Panzhou, Liupanshui, Guizhou (**A**); CIB 122558, Heilongtan Park, Kunming, Yunnan (**B, C**); Mengzi, Yunnan (**D**); Pugu, Panzhou, Liupanshui, Guizhou (**E**). Photographs by J.J. Huang (**A**) and M. L. Li (**B–E**).

Comparisons. The main diagnostic characters distinguishing *Hebius malnatei* sp. nov**.** from the 37 other congeners recorded from China and the Indo-Burma region (Vietnam, Laos, Cambodia, Thailand, and Myanmar) are summarized in Suppl. material 1: table S4. The new species is readily distinguished from all congeners by the frequent absence or extreme reduction of the anterior temporal scale to a minute or vestigial form; all other species possess one or two well-developed anterior temporals, except *H. atemporalis*, which also lacks this character.

Hebius malnatei sp. nov. differs from *H. andreae* (Ziegler & Le), *H. bitaeniatus* (Wall), *H. boulengeri* (Gressitt), *H. clerki* (Wall), *H. craspedogaster* (Boulenger), *H. deschauenseei* (Taylor), *H. gilhodesi* (Wall), *H. groundwateri* (Smith), *H. igneus* David, Vogel, Nguyen, Orlov, Pauwels, Teynié & Ziegler, *H. inas* (Laidlaw), *H. jingdongensis* Ma, Shi, Ayi & Jiang, *H. johannis* (Boulenger), *H. leucomystax* (David, Bain, Nguyen, Orlov, Vogel, Vu & Ziegler), *H. metusia* (Inger, Zhao, Shaffer & Wu), *H. miyajimae* (Maki), *H. modestus* (Günther),

H. octolineatus (Boulenger), *H. optatus* (Hu & Zhao), *H. popei* (Schmidt), *H. sangzhiensis* Zhou, Qi, Lu, Lyu & Li, *H. septemlineatus* (Schmidt), *H. shantianfangi* Liu, Wang, Hou, Zhang, Wang, Zong, Zhou, Rao, David & Vogel, *H. terrakarenorum* Hauser, Smits & David, *H. vibakari* (Boie), *H. vogeli* Nguyen, Li, Huang, Nguyen, Poyarkov & Ren, *H. weixiensis* Hou, Yuan, Wei, Zhao, Liu, Wu, Shen, Chen, Guo & Che, and *H. yanbianensis* Liu, Zhong, Wang, Liu & Guo by having 17 dorsal scale rows at midbody (vs. 19 in all compared species).

Hebius malnatei sp. nov. differs from *H. annamensis* (Bourret), *H. boulengeri*, *H. citrinoventer* Xu, Yang, Gong, Ouyang, Weng, Deng, Huang & Peng, *H. deschauenseei*, *H. gilhodesi*, *H. groundwateri*, *H. igneus*, *H. inas*, *H. optatus*, *H. terrakarenorum*, *H. venningi* (Wall), *H. vogeli*, and *H. youjiangensis* Yang, Xu, Wu, Gong, Huang & Huang in having a shorter relative tail length (TaL/TL 0.22–0.27 vs. ≥ 0.30).

The *Hebius malnatei* sp. nov. exhibits a higher number of ventral scales (VEN 146–156) than *H. inas* (VEN 141–148), *H. maximus* (Malnate) (VEN 132–143), *H. popei* (VEN 130–137), and *H. sauteri* (VEN 116–133), but fewer than *H. andreae* (VEN 179–180), *H. annamensis* (VEN 158–172), *H. chapaensis* (VEN 159–177), *H. clerki* (VEN 158–173), *H. igneus* (VEN 159–169), *H. jingdongensis* (VEN 163–166), *H. johannis* (VEN 156–179), *H. metusia* (VEN 159–164), *H. nigriventer* (Wall) (VEN 156–168), *H. optatus* (VEN 155–169), *H. sangzhiensis* (VEN 160–164), *H. septemlineatus* (VEN 164–175), *H. taronensis* (Smith) (VEN 158–175), *H. terrakarenorum* (VEN 159–171), *H. vogeli* (VEN 158–172), *H. venningi* (VEN 155–167), *H. yanbianensis* (VEN 159–175), and *H. weixiensis* (VEN 171–182), *H. youjiangensis* (VEN 160). Subcaudal scale count (SC 60–70) is lower than in *H. andreae* (SC 99–103), *H. annamensis* (SC 116–146), *H. bitaeniatus* (SC 76–89), *H. boulengeri* (SC 90–100), *H. chapaensis* (SC 90–114), *H. clerki* (SC 85–108), *H. citrinoventer* (SC 113), *H. craspedogaster* (SC 79–99), *H. gilhodesi* (SC 87–111), *H. inas* (SC 96–109), *H. deschauenseei* (SC 115–141), *H. igneus* (SC 115–129), *H. jingdongensis* (SC 71–74), *H. johannis* (SC 85–89), *H. leucomystax* (SC 95–109), *H. metusia* (SC 72–85), *H. miyajimae* (SC 87–92), *H. modestus* (SC 104–122), *H. nigriventer* (SC 105–143), *H. optatus* (SC 95–114), *H. octolineatus* (SC 70–80), *H. popei* (SC 69–88), *H. sangzhiensis* (SC 81–82), *H. septemlineatus* (SC 80–96), *H. taronensis* (SC 82–108), *H. terrakarenorum* (SC 107–130), *H. venningi* (SC 115–129), *H. vogeli* (SC 125–126), *H. weixiensis* (SC 74–88), and *H. youjiangensis* (SC 112).

In terms of dentition, *Hebius malnatei* sp. nov. has 26–29 maxillary teeth (MT), more than in *H. bitaeniatus* (MT 19–21), *H. clerki* (MT 18–22), *H. gilhodesi* (MT 21–23), *H. craspedogaster* (MT 20–25), *H. inas* (MT 20–21), *H. johannis* (MT 23–25), *H. jingdongensis* (MT 19), *H. miyajimae* (MT 20), *H. maximus* (MT 24), *H. metusia* (MT 23–24), *H. optatus* (MT 20–24), *H. sangzhiensis* (MT 21), *H. vibakari* (MT 21–25), *H. vogeli* (MT 25), and *H. yanbianensis* (MT 23–25), but fewer than *H. andreae* (MT 34), *H. chapaensis* (MT 29–34), *H. citrinoventer* (MT 31), *H. deschauenseei* (MT 29–36), *H. groundwateri* (MT 30), *H. igneus* (MT 29–30), and *H. youjiangensis* (MT 30).

Finally, *Hebius malnatei* sp. nov. differs markedly from *H. atemporalis*, its most morphologically similar congener, in several characters (Table 2): longer maximum SVL (416 mm vs. 294 mm), lower tail length ratio (TaL/TL 0.22–0.27 [mean 0.24 ± 0.01] vs. 0.28–0.33 [mean 0.30 ± 0.01]), higher number of ventrals (VEN 146–156 [mean 151.17 ± 3.27] vs. 123–140 [mean 130.87 ± 4.88]), higher combined ventral and subcaudal counts (VEN +SC 211–223 [mean 216.00 ± 4.14] vs. 198–209 [mean 203.45 ± 4.08]), dark olive coloration (vs. dark to reddish brown), and absence of a white or orange nuchal collar (vs. present).

Etymology. The specific epithet *malnatei* is a patronym in genitive declension honoring Edmond V. Malnate (1916–2003), an American herpetologist who made significant contributions to the taxonomy and systematics of Asian colubrid snakes, especially within Natricidae, and who first revised the taxonomic placement of *Hebius atemporalis*. We recommend the following common names for this species: English: "Malnate's Keelback", Chinese (中文): "云贵腹链蛇" (Yún Guì Fù Liàn Shé) for its restricted distribution to Yunnan-Guizhou Plateau. Vietnamese: "Rắn sãi Man-lát", French: "Couleuvre aquatique de Malnate", Russian (Русский): "Лесной уж Мэлнейта" (Lesnoy Uzh Melneyta).

Distribution. *Hebius malnatei* sp. nov. is likely endemic to China, with its known range restricted to the Yunnan-Guizhou Plateau at elevations of 1,750–1,950 m a.s.l. (Fig. 5).

Natural history notes. *Hebius malnatei* sp. nov. inhabits forests, shrubland, and meadows near ponds and streams (Fig. 8). The species is active both during the day and at night, with activity peaking around sunset. When captured by hand, individuals do not attempt to bite but invariably release a strong, fetid secretion from the cloacal glands as a defensive response. Earthworms are the only prey items recorded for this species to date. The holotype contained five well-developed oviductal eggs, indicating oviparity and suggesting a breeding season in late spring. *Hebius malnatei* sp. nov. is found sympatric with *H. octolineatus* and *H. johannis* based our field research in Kunming City, Yunnan Yunnan, China, but occupied different habitats, the latter two species are more aquatic, often found close to lakes and pounds.

Discussion

The integrative taxonomic evidence presented herein unequivocally supports the recognition of *Hebius malnatei* sp. nov. as a distinct evolutionary lineage within the *H. atemporalis* species complex. Morphological comparisons revealed a consistent suite of diagnostic characters (e.g., longer maximum SVL, higher ventral counts, shorter relative tail length, and absence of a nuchal collar) that reliably distinguish the new species from *H. atemporalis* sensu stricto. These findings are

Figure 8. Natural habitat of *Hebius malnatei* sp. nov. in Panlong, Kunming, China. Photograph by B.Y. Wu.

strongly corroborated by mitochondrial Cyt *b* data, with uncorrected *p*-distances of 8.0–9.8% between *Hebius malnatei* sp. nov. and *H. atemporalis* s. str. a level of divergence that falls well within the range of interspecific differences previously reported in *Hebius* (e.g., Guo et al. 2014; Hou et al. 2021; Ma et al. 2023). Together, these data justify the formal description of the Yunnan-Guizhou Plateau population as a new species.

Despite this advance, several issues remain unresolved. Certain populations from Yunnan historically referred to *Hebius atemporalis* were reported by Zhao et al. (1998), including three specimens from Yunnan Province, China: KIZ 79013 (male; VEN 132, SC 61) from Pingbian County, Honghe Prefecture; KIZ 7710072 (female; VEN 135, subcaudals unavailable) from Hekou County, Honghe Prefecture; and KIZ 75I352 (sex undetermined; VEN 149, SC 27+) from Menglian County, Pu'er City. Although we tentatively assign KIZ 79013 and KIZ 77I0072 to *H.* cf. *atemporalis* and KIZ 75I352 to *Hebius malnatei* sp. nov., these provisional placements highlight the need for direct examination and the collection of additional material. Similarly, a short and potentially contaminated Cyt *b* sequence attributed to *H. atemporalis* from Yunnan Province (GenBank accession KJ685695) was not analyzed in the present study. The sequence is unusually short (494 bp) and may be contaminated, highlighting the need for confirmatory sampling and sequencing before any taxonomic conclusion can be drawn. These ambiguous cases suggest that additional cryptic diversity may remain to be uncovered within the complex.

Furthermore, our analyses revealed relatively deep genetic differentiation (6.4–7.0% *p*-distance) between Chinese and Vietnamese populations of *Hebius atemporalis* s. str. Although morphological differences are subtle apart from higher maxillary teeth counts reported in the Hong Kong population (MT 32–36 vs. 27–30 in Tam Dao NP, Phu Tho Province, Vietnam) such divergence approaches thresholds commonly used to infer species-level separation in natricine snakes (Deepak et al. 2022). Whether these represent structured intraspecific lineages or as yet undescribed taxa remains uncertain. Broader geographic sampling coupled with multi-locus or genomic datasets will be essential to resolve this question. Within China itself, moderate genetic divergence (ca. 4%) between populations from Guizhou and Guangdong also suggests population structuring that may warrant further attention. In contrast, *H. atemporalis* is relatively more fossorial than its congeners. We hypothesize that this specialized ecology may restrict dispersal, potentially leading to the observed greater intraspecific genetic divergence, a premise that warrants further investigation.

From a conservation standpoint, the recognition of *Hebius malnatei* sp. nov. has important implications. Although currently known only from the Yunnan-Guizhou Plateau, its habitat appears relatively intact and no immediate threats are evident, supporting its preliminary assignment to the IUCN category Least Concern (LC). Nevertheless, given the species' restricted elevational range (1,750–1,950 m a.s.l.) and specialized habitat

association, targeted surveys and long-term monitoring are needed to assess its true distribution and population status. These efforts will be critical for anticipating potential vulnerability to habitat alteration and climate change in montane ecosystems. Furthermore, with the description of this new species, the conservation status of *H. atemporalis* s. str. also warrants re-evaluation.

Biogeographically, the divergence between *Hebius malnatei* sp. nov. and *H. atemporalis* s. str. (estimated at ca. 6.8 Ma; Deepak et al. 2022) corresponds closely to the major uplift phases of the Yunnan-Guizhou Plateau (Chen and Wang 2017). This supports a scenario of allopatric speciation driven by geological and climatic processes that generated complex topography and montane refugia. The region is increasingly recognized as a hotspot for cryptic amphibian and reptile diversity, with numerous lineages of Megophryidae Bonaparte, Rhacophoridae Hoffman, Colubridae Oppel, and Sibynophiidae Dunn showing similar patterns of local endemism (e.g., Li et al. 2013; Vogel et al. 2024; Nguyen and Vogel 2025). The discovery of *Hebius malnatei* sp. nov. reinforces the importance of the plateau as both a center of diversification and a priority area for biodiversity research and conservation.

In conclusion, the recognition of *Hebius malnatei* sp. nov. clarifies a longstanding taxonomic problem within the *H. atemporalis* complex, highlights additional unresolved diversity, and contributes to a growing body of evidence that the Yunnan-Guizhou Plateau functions as a cradle of herpetofaunal speciation. Future studies integrating multi-locus phylogenetics, population genomics, and detailed morphological analyses across broader sampling will be indispensable for resolving the taxonomy of this complex and refining conservation assessments for its constituent lineages.

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Supplementary material 1

Additional information

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Data type: docx

Explanation note: This file contains four supplementary tables, including GenBank accession numbers of sequences used in this study (table S1), museums, private collections and biorepository abbreviations (table S2), uncorrected genetic distances (table S3), and comparison of morphological characters (table S4).

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